COURTSHIP AND MATING OF BUTTERFLIES

STEPHEN F. HENNING

1 Harry Lawrence Street, Florida Park, Florida 1709, South Africa.

THE MOST important function of an adult butterfly is the continuation of the species. All their behaviour is geared towards this end. Each species has a particular type of behaviour so that males and females can locate or find each other. Having located each other a specific courtship ritual now takes place to ensure that the prospective mate that has been found belongs to the same species and is receptive to mating. Only at the completion of courtship will mating finally take place.

Although various aspects of sexual behaviour of a number of butterflies have been studied (Scott, 1968, 1967, 1974; Shields, 1967; Shields & Emmel, 1973), only a surprisingly small number of species have had their entire courship patterns observed and described. The females of many species tend to remain in the general vicinity of the larval foodplant, and males presumably seek out these areas for courtship. On the other hand, males of the Lycaenidae in particular, but other families too, often gather on nearby rises of hill-tops where they "stake out" a little territory which they protect, and the females come up to these hill-tops to find a mate.

Visual recognition of the female by the male is of great importance in bringing the sexes together, but no one knows much about just how important the visual, tactile, chemical and acoustic stimuli are, relative to each other, in bringing the sexes of one species together. Entire courtships ending in mating are rarely seen at close quarters in nature, and there has been little experimentation in the field or in large cages.

Mate-locating

Mate-locating behaviour is defined as behaviour which brings the sexes together for mating. It includes the methods used to find mates, the location of mating, and the time of day of initiation of mating (Scott, 1974).

Chemoreception is known to be very important in the long-distance location of females by males in moths, and in the courtship of moths and butterflies. It may possibly prove to be important in location of females by males in the Acraeidae as well. For most butterflies, however, the maximum distance of attraction is limited by sight, while chemoreception is important only within a few metres of the females by the release of pheromones from hair pencils, androconial scales and so on.

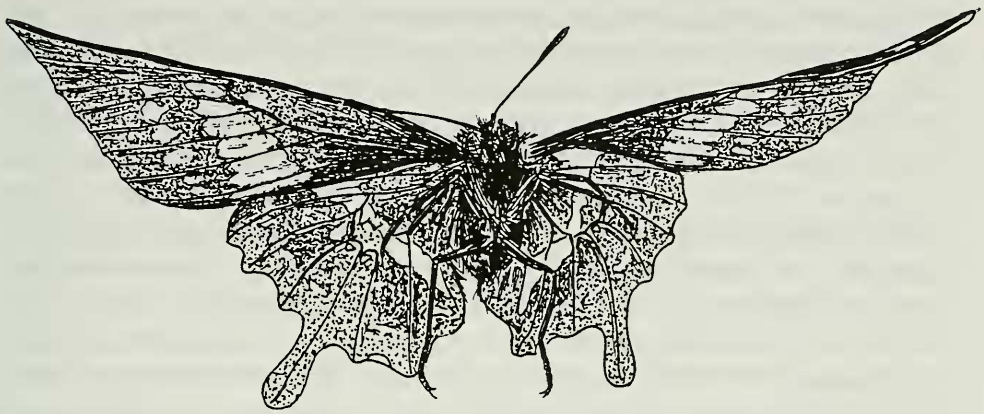
There are two main types of mate-locating behaviour in butterflies. The first is perching behaviour which is defined as a mate-locating method in which males sit at characteristic sites and dart out at passing objects in search of females. The females generally fly to these sites to mate, then they depart. The second is patrolling behaviour, a mate-locating method in which males fly almost constantly in search of females.

Movement, size, wing colour, wing pattern, and odour are stimuli which can be transmitted during sexual communication in the approach of a male to a female. Perching males are highly attracted to moving objects, whereas patrolling males often are attracted to motionless objects resembling females in some way. Perching species usually mate in limited areas of habitat, often during only part of the day, whereas patrolling species usually mate throughout the habitat at any time of day.

Territoriality is usually exhibited by males which perch or patrol in a particular beat or area. They will investigate and challenge not only other males of the same species that enter the territory but other appropriately sized flying insects as well. The resident male most frequently succeeds in his challenge. Virgin females entering a territory are at once pursued and courtship commenced. In the case of many Hesperiidae and Lycaenidae a particular male will have a favoured perch or perches in its territory on which it will settle, often returning after an encounter to the exact spot from which it launched itself. If that individual is caught it may be replaced within minutes or hours by another individual of the same or a different species. Surprisingly, the new individual may rest on or near the same twig as its predecessor. Evidently there are certain particularly favoured spots in any small area of habitat and these are occupied in preference to others. On the other hand, in some species (eg *Papilio demodocus* Esper) the males patrol for long periods and perch only briefly. The males seldom engage in feeding activities while they are perching or patrolling. Since they appear only as the day warms up, they probably go nectar-gathering before starting their territorial behaviour.

Both perching and patrolling species also exhibit other types of behaviour which help the sexes to locate each other. The most noticeable is hill-topping behaviour in which males of low-density species fly to the summits of hills and there show perching or patrolling behaviour. In these species the males ascend to the hill-tops to be in a conspicuous spot so that the newly hatched females might fly kilometres without finding a mate if they tend to be sparsely scattered. So the female goes up to the top of the hill, very soon gets fertilised and goes away again and almost never returns (Scott, 1968).

Hill-topping low density species have many behavioural traits in common. They do not congregate about the foodplant but instead tend to be large, strong-flying, solitary species. When a specimen of these low density species emerges from the pupa it will be unlikely to find a member of the opposite sex in the near vicinity. If unable to find a mate it will ascend to the highest topographic point where it will find other members of the same species which will also have ascended to the peaks to mate. The males which will mate more than once tend to congregate around these high points waiting for females. A high proportion of females only mate once or twice in their lives, therefore many will only ascend to the summit shortly



Papilio euphranor Trimens, a montane forest species shown patrolling, gliding back and forth at considerable height in clearings above valleys and waterfalls.

after emerging and once mated will never return. This is why females are seldom observed on the summits as they are only there long enough to mate. Courtship usually only lasts two to three minutes and once *in cop* they are usually out of sight in the grass or in a tree often downhill from the summit. So chances are very slight that you will see a female. This gives rise to the impression that only the males are hill-topping. *Charaxes jasius saturnus* Butler is a good example of a low density species that shows hill-topping behaviour. It is an extremely common butterfly in the bushveld of South Africa but is regarded as a low density species as its foodplants are scattered throughout the bush and the females range widely laying their eggs wherever they find a suitable tree (Henning, 1989).

During hill-topping the males may either perch on a shrub, tree or patch of ground (eg *Iolaus trimeni* Wallengren) or patrol back and forth on the summit (as in *Papilio demodocus* Esper). The behaviour of hill-topping species is not fundamentally different from other species; hill topping behaviour occurs when these activities are transferred to a hill-top. Perching males may well remain on a hill-top for several days.

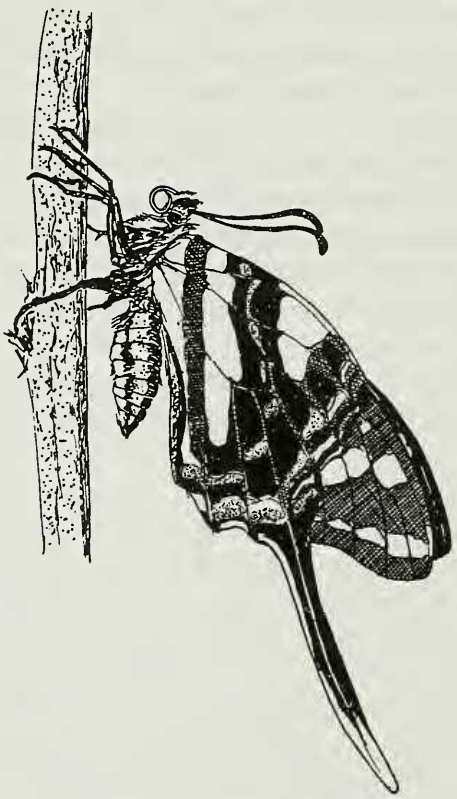
The males, which usually emerge earlier than females, visually orientate and fly to the hill-tops where each will stake out a little territory which he will defend against challengers of his own species (or even other species if they look similar). The females, when they emerge, also fly to the hill-tops, mating occurs, and then the females leave to lay their eggs and almost never return. Nearly all females found flying on the hill-tops will be virgins searching for mates. Usually there is no foodplant to lay their eggs on up on the hill-tops, nor is there much nectar to eat. This means that the males must feed further down in the valleys before coming up to the hill-tops. Species differ in their time of arrival on a hill-top and may stay until quite late in the afternoon. Certain hill-tops are consistently favoured over others

nearby but no one knows yet why some seem more preferable than others.

It appears that hill-topping behaviour can be effective only for low density species, because at high densities on hill-tops interference between males prevents mating with females and the number of hill-tops is limited. If a species is common, only a small proportion of the males can occupy a hill-top, so that most males will be forced into non hill-top situations. As population density rises, the probability that a female will meet a male before reaching a hill-top therefore increases, so that hill-topping is less important for commoner species. The few males on hill-tops could not possibly inseminate all the females in a common species, so that most matings will occur with males which remain at the breeding site or which are between the breeding site and the hill-top. Because hill-topping is less useful for common species, selection should eliminate the hill-topping response since males which remain at the breeding sites will contribute more genes to the next generation.

Hill-topping species are then in general large, fast-flying, solitary species with more widely scattered and less abundant foodplants than non hill-topping species, which tend to be small, weak-flying, colonial species with common or clumped foodplants.

Of the non hill-topping species most of them, especially the weak fliers, spend their entire lives, except for brief forays in search of mud or flowers



Graphium junodi (Trimen) patrols for long periods and perches only briefly.

for nourishment, around stands of the foodplant, and therefore have a built-in mechanism for bringing the sexes together. Often the sexes are limited both to foodplant and to certain areas of the environment such as marshes, rockslides, or forests, which may or may not be the only locations of the foodplant. The behaviour of these species usually limits them to these areas so that mating is possible with "random" flights by both sexes or by patrolling of the area by males.

In myrmecophilous species they will be confined to the foodplants in a particular area because it is only here that the host ant occurs. This will include all the myrmecophilous species such as the *Lepidochrysops*. In these species when an individual emerges from the pupa it is very likely to encounter a member of the opposite sex since they will also emerge from the same or nearby ant nests. Therefore in these species you will generally find that most mating will occur in the vicinity of the foodplants. These species will benefit from hill-topping only when their populations fall to low levels. Hill-topping may be selected for at low population levels, and remaining near the foodplant may be selected for at high levels, so that the advantage of hill-topping for a particular species could depend on its average density and the fluctuation from this average. In swarm years which often occur in some species such as *Lepidochrysops robertsoni* Cottrell excess males displaced from territories around the foodplants and ants' nests may ascend to nearby hills in the hope of the appearance of a mate, but the vast majority of mating will occur near the foodplants.

In some species the males occupy small areas along the bottom of a gully or gorge, presumably for mating purposes. Males may occupy an area for some time, but this behaviour may not be territorial since the males may wander to another gully and show the same behaviour. A group of butterflies which show this behaviour are the *Poecilmitis*.

The males of rainforest species usually show perching and patrolling behaviour in forest clearings, roads or along the outskirts of the woods.

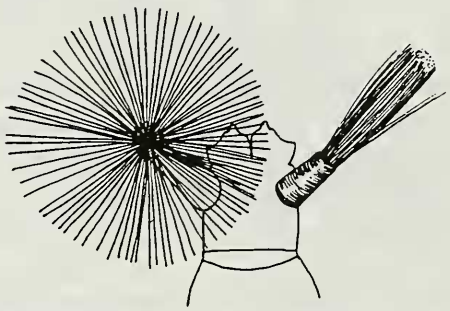
Courtship

There is a tremendous diversity of courtship behaviour. In patrolling species, the two sexes may meet during flight or the flying male may meet a female at rest. In perching species, the female flies near the male, who then pursues her. Subsequent events can be divided into aerial events and ground events although in some species identical activities may occur in the air and on the ground or plant. In the aerial phase, which is omitted altogether in some species, the two sexes often merely flutter about each other, or fly in stereotyped patterns, or one or both sexes may perform specialised acts for transferring pheromones. The aerial flight usually results in the female alighting, whereupon the receptive females of some species usually become inactive until copulation occurs. Unreceptive females of some species may flap their wings or fly a special pattern

(rejection dances), or adopt a special rejection posture. After the female alights, the male may continue to fly about the female, or may land, whereupon one or both sexes may still flutter their wings, and the male may perform complicated manoeuvres with his wings, antennae, or legs. Copulation may then occur, or various courtship events may then be repeated.

Pheromones of one or both sexes are important in the courtship of most species although only in the Danaidae have pheromones been chemically identified. Pheromones are substances, produced by one individual, that influences the behaviour of other members of the same species. It is well known, for example, that the virgin females of many moth species produce a powerful and specific sex pheromone that is capable of attracting her specific mate from distances of hundreds if not thousands of metres. In some species of moth, when the male gets close to the female he releases an aphrodisiac pheromone which brings about mating. Amongst butterflies it is usually the male, instead of the female that possesses scent organs. These may be highly modified scales or pouches on either the fore or hind wings, or special little structures on the abdomen. Sex brands, which are formed of these specially modified scales and which also produce scents, occur in many butterfly species.

The most highly developed male scent organs are found in the Danaidae. These organs are the paired hair-pencils (they look like pencils made up of lots of little hairs in a cylinder). These pencils can be pushed out from the tip of the abdomen and release a pheromone during courship. In some species the hair-pencils are covered with fine dust-like particles which shower forth as a rain of scented particles when the hair-pencils shoot out. There are also conspicuous wing glands which, with the hair-pencils, produce pheromones that are a characteristic for each species so that the butterflies can tell their own species from all the others. Some of these pheromones can even be detected by the human nose.



Tip of abdomen of Danaus chrysippus (Linnaeus) showing scent brushes (hair-pencils), with one open and one closed.

Stride (1958) watched *Danaus chrysippus* (Linnaeus) courtship and he noticed that, while the female normally flies in a leisurely, unhurried manner, during courtship she adopts a rapid, rather jerky flight. On

overtaking the female the male flies above, hair-pencilling the front part of the female every time an opportunity presents itself. Within a short time, the female settles with the male beside her facing in the same direction.

Then the male bends his abdomen sideways to reach the female and join with her. If, during mating, flight becomes necessary, the male flies carrying the female with him, not as in some other butterflies where the female is the active partner.

In most other species, the pheromone is only used when the butterfly is one or two metres from its partner, but not further away. Female pheromone evokes the male pursuing response and causes continued courtship, while the male pheromone may cause the female to land and accept the male.

Mating

To initiate copulation the males of almost all butterflies grasp the female from a position slightly behind her while facing the same direction as the female and bending his abdomen right or left 180° to grasp her abdomen. Then the male moves sideways until the partners face opposite directions.

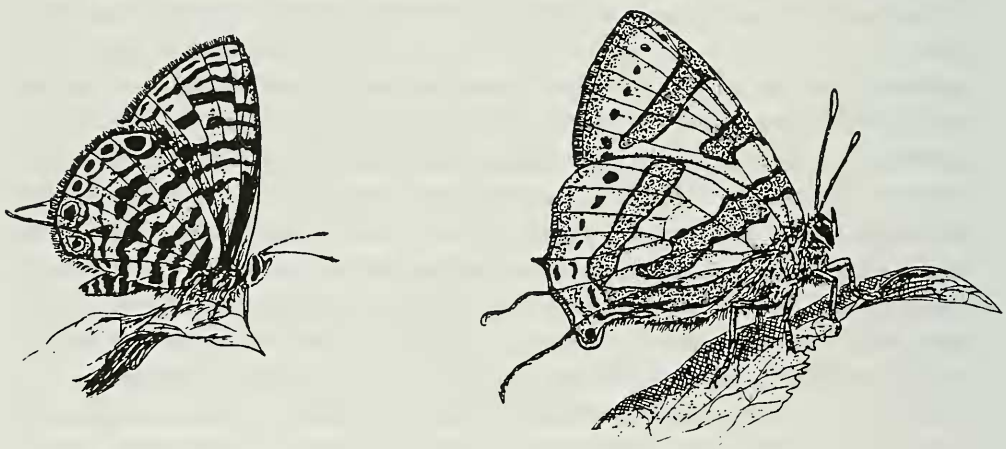
The pair remain at the mating site, where they may separately or both bask in the sun by opening their wings, or may fly if disturbed. If disturbed, the sex which carries the other is usually fixed within the species and it will fly, carrying the other behind. In species in which only one sex carries the other, the active sex usually positions itself above the other, with its wings outside of those of the other, and is more likely to walk during copulation. The inactive sex remains in a state of immobility known as catelepsis. At the end of copulation in *Precis* the female kicks and turns until the male is broken off; then the male flies away. In other species the male initiates uncoupling. Apparently only in the Danaidae is there a postnuptial flight (the male always carries the female a short distance).

Copulation lasts about half to three hours depending on the species, and occasionally overnight. Copulation is longer at lower temperature and if the male has recently mated. Males can mate five times or more, whereas the number of matings per female varies between species from only once to an average of three.

In some species a large structure known as the sphragis is deposited by the male in the copulatory opening of the female preventing further mating. A sphragis is known in Acraeidae and Danaidae (*Amaurus*). In all the species with a large sphragis, many similarities exist, including the absence of courtship, powerful odour (pheromones) of adults of both sexes, and strong attraction of males to virgins. The male captures the female without any courtship in the Acraeidae and it appears that the females produce an attracting pheromone. It appears that the large sphragis serves to inhibit the emission of the female pheromone. The male of these species can easily detect whether the female is virgin or mated by

physically detecting the sphragis (or because of pheromones) and he can therefore mate immediately without wasting time courting. In other butterflies, determining the receptivity of the female may not be so easy, and one function of courtship is to increase the female's receptivity so that mating can occur.

Females can mate the first day of adult life in almost all species, although they may mate more readily after a day or two. In contrast, males usually mate only after several days. Males often develop distinctive odours (male pheromones) only after a few days. Females of perching species often must fly to the mating site, so may be older than patrolling species at first mating. The difference between the sexes in minimum age of mating is due to three reasons. Males almost always take the active role in mate-locating, so must be capable of stronger flight, so must wait a few days before actively perching or patrolling. Second, it is advantageous to fertilise the females as soon as possible in the usual preoviposition period so that the time for oviposition is not reduced. Finally males almost always emerge a few days before females.



Cyclyrius babaulti (Stempffer) perching on a leaf (left) and *Iolaus (Epamera) diametra natalica* Vári which perches along forest roads, clearings or along the outskirts of the woods (right).

References

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